

# Recognition of breeding populations in foraminifera: an example using the genus *Glabratella*

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**Abstract.** Four morphospecies of foraminifera, *Glabratella opercularis*, *G. subopercularis*, *G. nakamurai*, and *G. patelliformis*, all of which have similar test morphologies, were reclassified by the use of both morphological characters and interbreeding experiments. Because specimens of *Glabratella* have been shown to reproduce sexually, it should be possible to determine breeding populational boundaries within *Glabratella* and to compare these with morphologically based taxonomic boundaries.

Using stable characters, three morphogroups were reclassified from the four morphospecies. Laboratory interbreeding experiments revealed that individuals belonging to the same morphogroup formed gamontogamous pairs and then reproduced. However, individuals belonging to different morphogroups did not produce any gamontogamous pairs. This indicates that each of the reclassified morphogroups represents a distinct breeding population.

Within the same morphogroup, individuals collected from two different localities closer than 100 km apart could interbreed with each other. However, individuals from more than 500 km apart could not breed with each other, even though the morphological characters of the individuals were very similar. This suggests that the population structure of the *P. opercularis* morphogroup is very similar to those of ring species.

**Key words:** benthic foraminifera, breeding populations, interbreeding experiments, morphospecies, ring species

## Introduction

Conventionally, the species-level systematics of foraminifera have been carried out only with morphological characters of the test. Recently, biogeographic data, indicating areal and depth distributions in the sea, have also been used for defining foraminiferal species in addition to morphological data (e. g., Matoba, 1970). Fifty or sixty thousand foraminiferal morphospecies, both modern and extinct ones, have been described (Bock *et al.*, 1985; Loeblich and Tappan, 1988; Culver, 1993). However, doubt remains whether or not foraminiferal species defined by test morphologies are equivalent to breeding populations that can interbreed within a morphologically defined population (Boltovskoy and Wright, 1976).

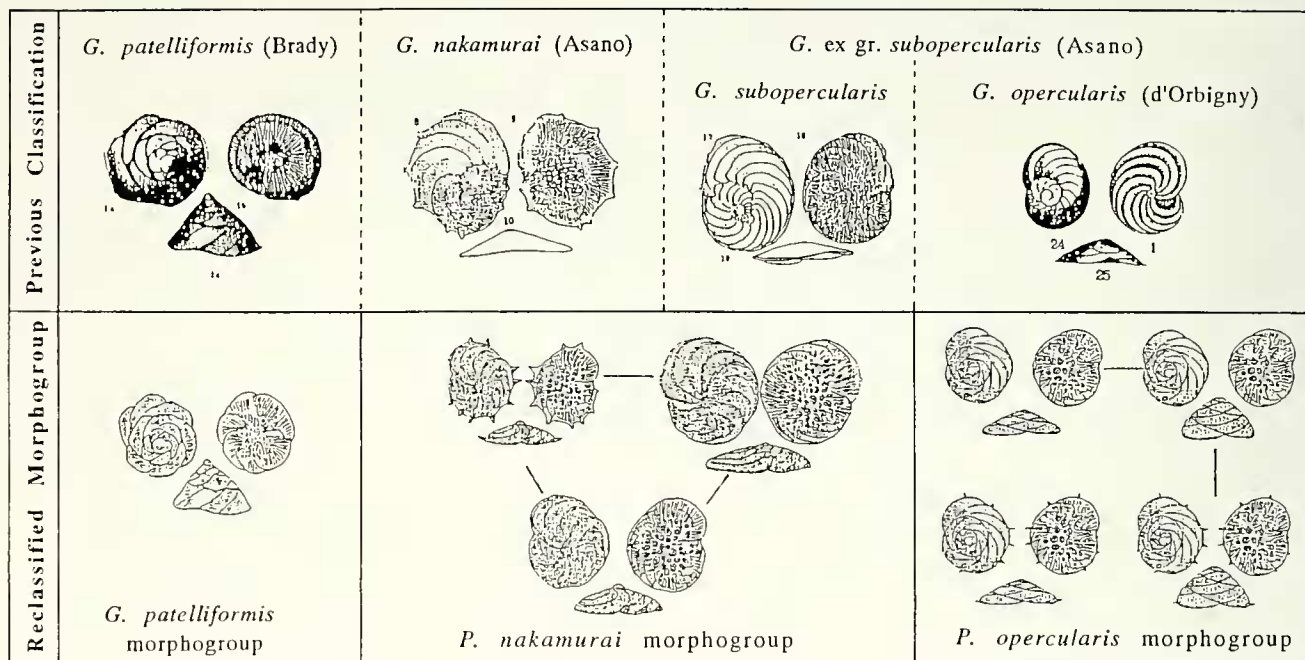
According to the definition of Mayr (1969), a species is the array of populations that are actually or potentially able to interbreed and that are reproductively isolated from other such arrays under natural conditions. This definition is mainly appropriate for metazoan taxa with two sexes, and it is problematic to adopt this concept to protistan taxa, which have both sexual and asexual reproduction during their life cycles.

How should we define species among protistan taxa?

Sonneborn (1957) discussed the species concept in Protista. He carried out breeding experiments within a *Paramecium* species complex that enabled him to recognize breeding populations that could form conjugation pairs. He called this "breeding population" a "syngen". A "syngen" may be comparable to a "species". However, there still exists much controversy about the nature of species in protistan taxa, in particular foraminifera (Boltovskoy, 1954; Grell, 1959; Nyholm, 1961; Schnitker, 1974; Tendal, 1990).

In this study, as a first step toward solving the species problem in foraminifera, we have examined whether morphologically based species have the same boundaries as breeding populations for foraminifera. Breeding populations of *Glabratella* can be recognized rather easily, because specimens of this genus have been observed participating in sexual reproduction through formation of gamontogamous pairs (Myers, 1943). Observation of sexual reproduction is a positive method for determining the degree to which populations interbreed in foraminifera.

Sixteen morphospecies of *Glabratella* are known from the sea adjacent to the Japanese Islands (Matoba, 1970;



**Figure 1.** Four selected morphospecies of *Glabratella* that exhibit similar test morphologies. Original illustrations are shown in the upper panel. Reclassified morphogroups are shown in the lower panel. Not to the scale.

Kanesaki, 1987MS). Most of them live in the intertidal zone of rocky shores. They crawl on leaves or thalli of seaweeds and graze microalgae or organic detritus on the surface of seaweeds (Kitazato, 1984, 1988, 1994). Among these *Glabratella* species, *G. nakamurai* (Asano), *G. opercularis* (d'Orbigny), *G. patelliformis* (Brady), and *G. subopercularis* (Asano) have similar test morphologies (Figure 1). Some specimens have mixed morphological characters of two species. Thus, it is sometimes difficult to identify specimens at the species level. In this study, we tried to reclassify these four morphospecies by making use of both morphological characters and the results of interbreeding experiments in the laboratory.

#### Methods of study

Samples for the study were collected from the intertidal zone of rocky shores adjacent to the Japanese Islands (Kanesaki, 1987MS). Living individuals were collected at tide pools in Omaezaki Cape (34°36'N, 138°14'E) and Shimoda Bay (34°39'N, 138°57'E), both in Shizuoka Prefecture, central Japan. Additional samples were collected at tide pools in Oshika Peninsula, Miyagi Prefecture (36°15.0'N, 136°08.4'E) and Echizen-Matsushima Coast, Fukui Prefecture (38°23.9'N, 141°24.7'E) for interbreeding experiments among different localities. Sampling localities are shown in Figure 2.

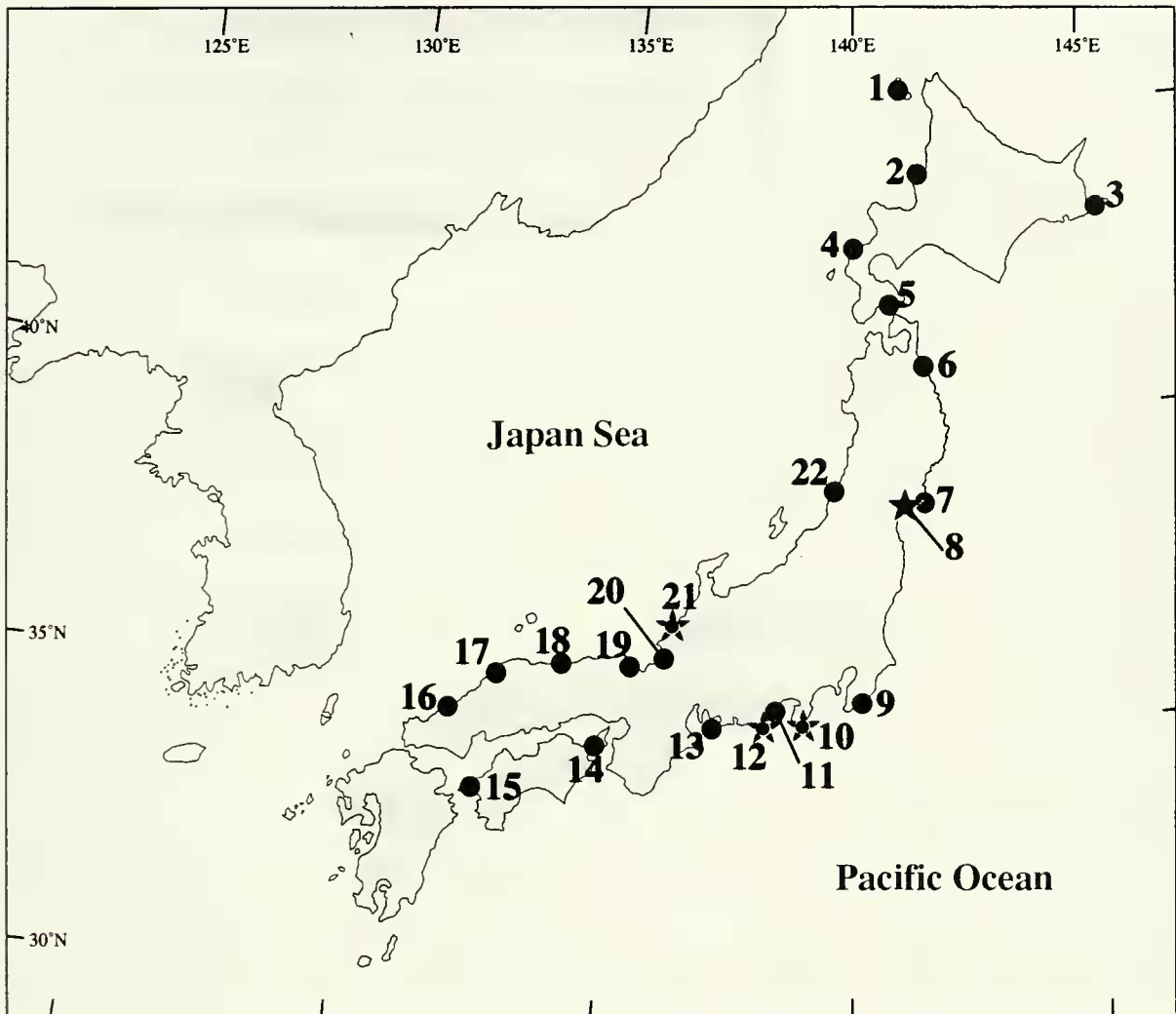
Two approaches were used during the course of this study. Firstly, we carefully observed the ontogeny of test morphologies of *Glabratella* morphospecies, both of agamont and gamont specimens, using a scanning electron

microscope.

Secondly, culture experiments were carried out to examine the breeding ability of reclassified morphogroups. Seaweed with attached living foraminifera was collected from tide pools and placed in large culture tanks filled with well oxygenated sea water (Kitazato, 1984, 1988). Living foraminifera were transferred from the culture tank into a small petri dish for observation under a binocular microscope.

Individuals were cultured in petri dishes. A diatom species, *Navicula* sp., was isolated from the tide pool of the Omaezaki Cape, cultured, and used as a food source. *Glabratella* spp. ate little of other single-celled algae such as *Chlorella* and *Dunaliella* (Chlorophyceae), *Amphiprora* (Diatomophyceae) and *Cryptomonas* (Cryptophyceae) species.

Both intraspecific and interpopulational breeding experiments were carried out using a small petri dish. Two individuals, each collected from a different locality or different morphogroup, were placed on a small petri dish (28mm inner diameter) with fresh seawater. The formation of a gamontogamous pair was observed in the petri dish using a phase-contrast apparatus attached to an inverted microscope (Nikon-TMD Cultivation Microscope System and Olympus IMT-2 Inverted Microscope System). An automatic microphotographic system (Nikon-HFM) attached to the inverted microscope was used to record the process of gamontogamy. Interspecific breeding experiments by three morphospecies were carried out using a large petri dish (87mm inner diameter). Twenty gamont individuals of the three morphogroups were mixed in a petri dish and ob-



**Figure 2.** Map showing sampling localities. Closed circles indicate localities for measuring height/diameter ratio of *Planoglabratella opercularis* morphogroup. Asterisks are localities where interpopulational breeding experiments were carried out. 1. Rebuntou. 2. Rumoi. 3. Nokamappu. 4. Biya. 5. Kattoshimisaki. 6. Hachinohe. 7. Hamagurihama. 8. Oshika Peninsula (Sendai Bay). 9. Kamogawa-Bentenjima. 10. Shimoda (Ooura). 11. Obama. 12. Omaezaki. 13. Irakomisaki. 14. Yoroizaki. 15. Takaura. 16. Tsuchida. 17. Futamata. 18. Nagawase. 19. Momojima-Nishi. 20. Hayase. 21. Echizen-Matsushima. 22. Kobato.

served almost continually until individuals formed gamont-gamont pairs. It is easy to distinguish specific morphogroups under a binocular microscope.

## Results and discussion

### Morphological observations

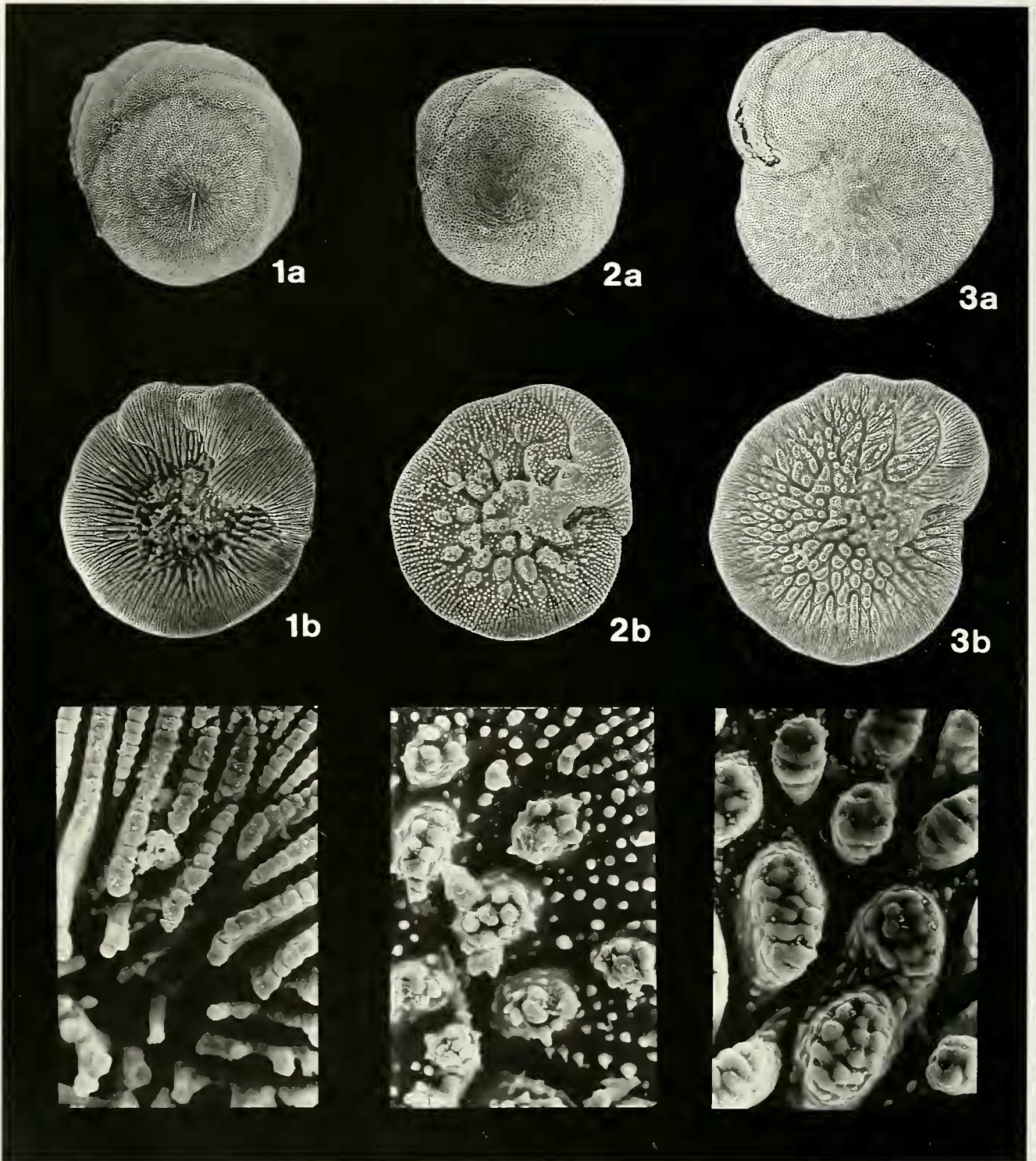
*Glabratella* species have trochospiral, spiroconvex, and conical tests. The umbilical side is flattened with a slightly depressed umbilicus. The surface of the spiral side is rugose. The umbilical side is ornamented with rows of pustules that form radially aligned striae. Sutures are flush with the surface on the spiral side in general, but depressed on the umbilical side. The aperture opens at the interiomarginal part of the ventral side of the ultimate chamber of the

test. The aperture is an arched slit that is bordered by a weakly developed rim. Radial striae, which form groove and ridge systems, are developed on the ventral face. Radial striae probably have a function related to rhizopodial activity during movement or feeding (Kitazato, 1992).

These morphological characters are common to all four morphospecies. They are also common to both agamont and gamont individuals, although the test size of the agamont is about twice as large as that of the gamont.

Several kinds of sculpture on the ventral side of the test, such as tubercles, radial granules, and crenulation of the suture line between chambers, together with surface relief and basic chamber shapes, are stable during ontogeny in each morphogroup (Figure 3). We tried to reclassify *Glabratella* morphospecies into several morphotypes using





**Figure 3.** Overview of test morphologies of three morphogroups of the genus *Glabratella*. Dorsal (a) and ventral (b) views and enlargement of ventral surface (c) are shown for 1-4. **1a-c.** *Glabratella patelliformis* morphogroup. **1a.**  $\times 94$ . **1b.**  $\times 94$ . **1c.**  $\times 540$ . **2a-c.** *Planoglabratella opercularis* morphogroup. **2a.**  $\times 94$ . **2b.**  $\times 94$ . **2c.**  $\times 540$ . **3a-c.** *Planoglabratella nakamurai* morphogroup. **3a.**  $\times 86$ . **3b.**  $\times 78$ . **3c.**  $\times 600$ .

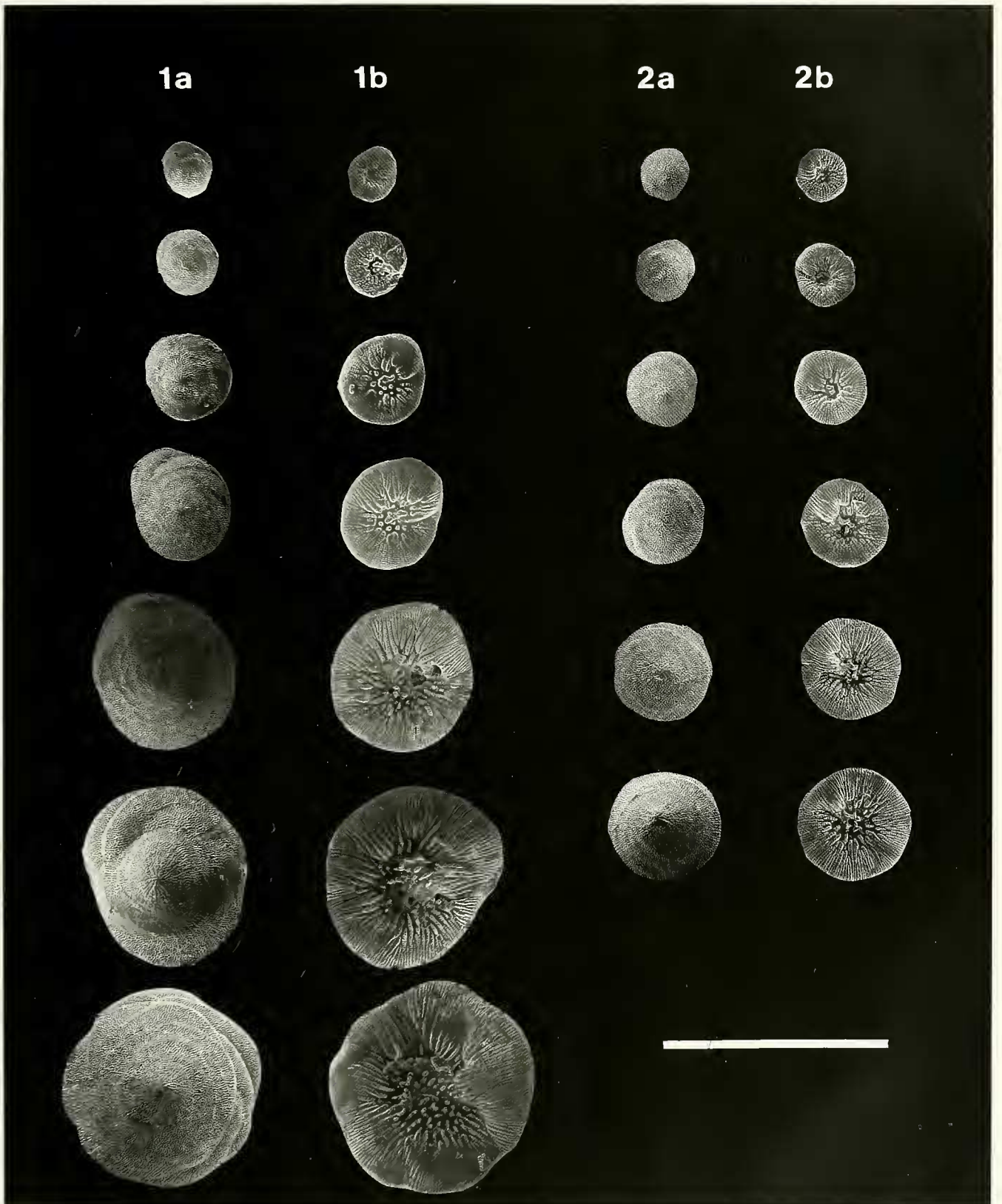


Figure 4.



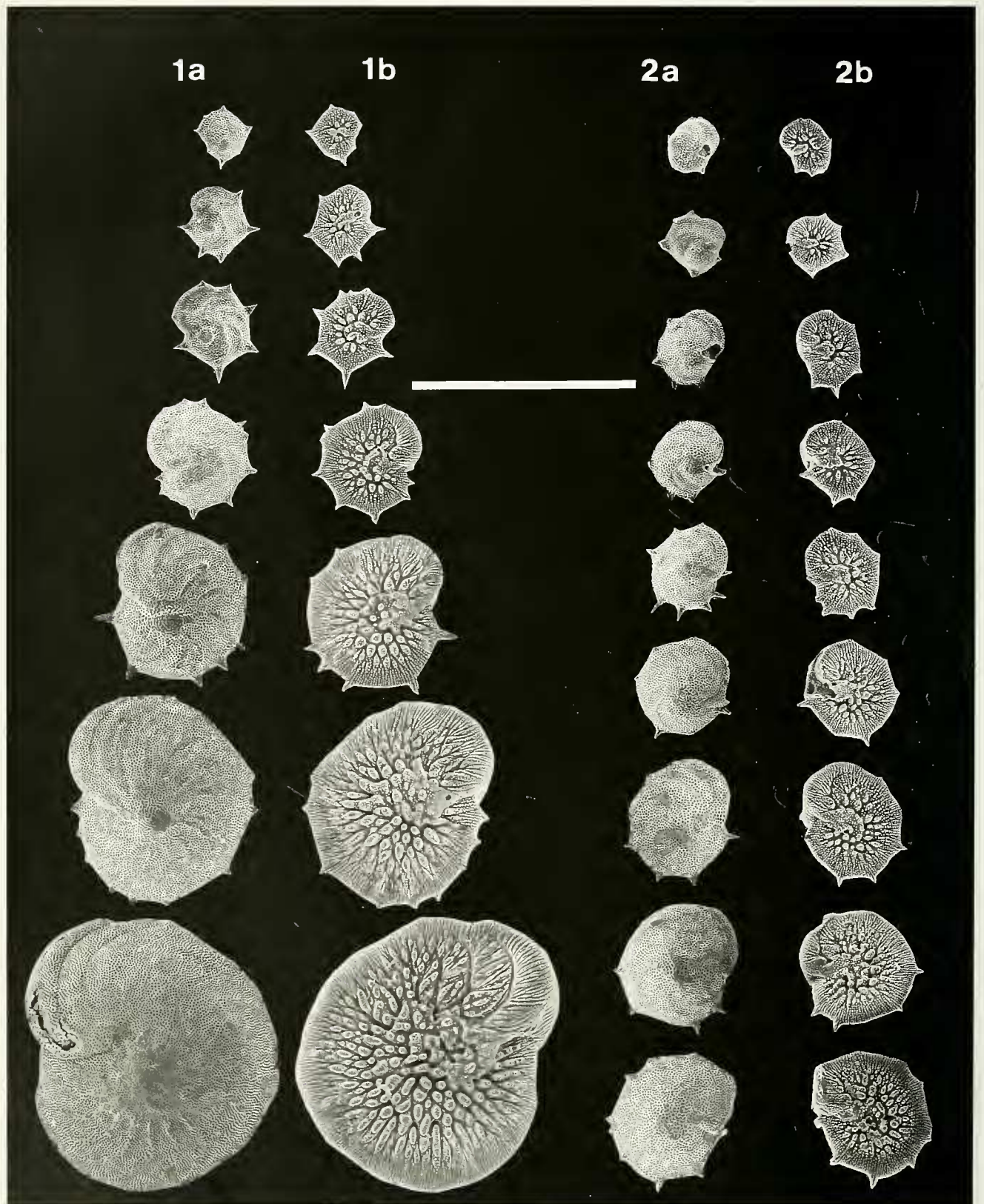


Figure 5.

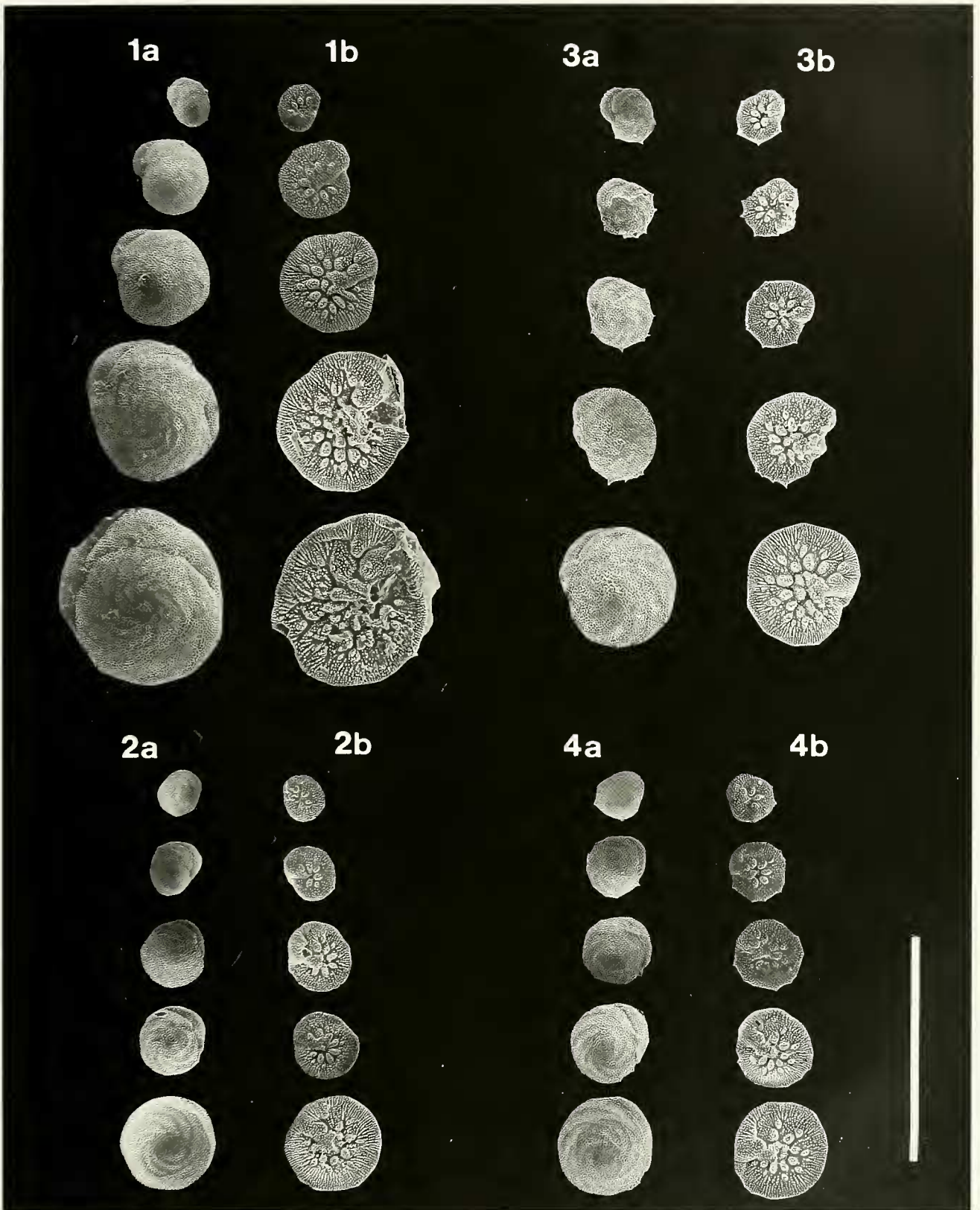


Figure 6.



only these stable morphological characters.

The four morphospecies were reclassified into three morphogroups (Figure 1). The characters of each reclassified morphogroup are as follows.

i) *Glabratella patelliformis* morphogroup (= *Discorbina patelliformis* Brady, 1884): This morphogroup is characterized by a strongly crenulated suture line between chambers, radial ridges made from a straight arrangement of needles, and needlelike tubercles at the center of the ventral side (Figure 3.1a–c).

ii) *Planoglabratella opercularis* morphogroup (= *Discorbis opercularis* d'Orbigny, 1839): This one is characterized by having rather smooth suture lines in comparison to *G. patelliformis*, sparsely arranged radial ridges, and spiny tubercles on the central area of the ventral side (Figure 3.2 a–c). Recently, Loeblich and Tappan (1988) separated flat *Glabratella* species from genus *Glabratella*, and established *Planoglabratella* as a new generic name. Here, we apply the new generic name to *G. nakamurai* and *G. opercularis*, following Loeblich and Tappan (1988).

iii) *Planoglabratella nakamurai* morphogroup (= *Discorbis nakamurai* Asano, 1951): This morphogroup is characterized by simple bowl-like sutures, radial ridges only at the peripheral part of the ventral side, and tough flamboidal tubercles that cover most of the ventral surface (Figure 3.3a–c).

These morphological characters are present continuously through all growth-stages within the same morphogroup (Figures 4–6). These characters are also continuously present in both gamont and agamont tests, even though gamont and agamont test sizes are different.

Several morphological characters such as peripheral spines, height/diameter (=H/D) ratio and others vary with growth and also with the ambient environment. Peripheral spines of *P. nakamurai* disappeared in later growth stages, becoming covered by nonspinose chambers (Figure 5). The involutely coiled whorl in *P. nakamurai* sometimes becomes evolute at maturity. The mature stage of *P. nakamurai* is quite similar to the holotype of *G. subopercularis* (Asano). Thus, we regard *G. subopercularis* as a junior synonym of *P. nakamurai*.

The height/diameter ratio of the test of *P. opercularis* varies from locality to locality. The H/D ratio of populations in the Japan Sea was higher than in the Pacific (Figure 7). The H/D ratio at each locality was calculated from the slope of linear regression of height against diameter from one population. One hundred specimens were measured at

each locality. Along the Pacific, a population from Omaezaki Cape showed a higher mean H/D ratio than one from Ooura in Shimoda Bay (Figure 7). The H/D ratio also varied seasonally (Figure 8). The difference in H/D ratios of allopatric populations was larger than the seasonal fluctuations at one locality.

Like *P. nakamurai*, there are both spinose and nonspinose individuals of *P. opercularis* (Figure 6). However, peripheral spines of this morphogroup appeared at all ontogenetic stages (Figure 6.3, 6.4). This phenomenon was not observed in *P. nakamurai*. This morphological variation in *P. opercularis* also appeared in all localities around the Japanese Islands. Geographic variation in the proportion of spinose and nonspinose individuals in individual populations has not yet been analyzed.

### Interbreeding experiments

Interbreeding experiments were carried out among three morphogroups that were reclassified based on morphological characters to examine whether or not these morphogroups represented interbreeding populations. Interbreeding experiments were also made among populations of *P. opercularis*, which are distributed in remote localities along the Japanese Islands.

Formation of a gamontogamous pair progressed as follows (Figure 9):

- 1) When two individuals came near enough to reach each other by rhizopodia, they immediately extruded a bundle of rhizopodia between them (Figure 9.1).
- 2) They maintained contact via these bundles for a few minutes, but the tests remained at some distance from each other (Figure 9.1).
- 3) After a few minutes they pulled each other until their tests touched (Figure 9.2, 9.3).
- 4) Still connected by the bundles, they lifted their tests and stuck themselves together along their ventral sides (Figure 9.4–9.8). Subsequently, most of the rhizopodia were withdrawn into the paired tests. To form a gamontogamous pair took approximately one hour on average. The exchange of gametes took place directly between the pair. We could not directly observe exchange of gametes between a pair through the tests, because *Glabratella* tests are too thick-walled and thus not transparent enough. Two-chambered agamontic juveniles appeared outside the pair one or two days after pair formation.

The processes of constructing a gamontogamous pair in

**Figure 4.** 1–2. Ontogeny of both agamont and gamont of *Glabratella patelliformis* (Brady). Collected at Omaezaki Cape, Shizuoka Prefecture. Scale bar indicates 500  $\mu$ m. **1a.** Dorsal view of agamont. **1b.** Ventral view of agamont. **2a.** Dorsal view of gamont. **2b.** Ventral view of gamont.

**Figure 5.** 1–2. Ontogeny of both agamont and gamont of *Planoglabratella nakamurai* (Asano). Collected at Hayama, Kanagawa Prefecture. Scale bar indicates 500  $\mu$ m. **1a.** Dorsal view of agamont. **1b.** Ventral view of agamont. **2a.** Dorsal view of gamont. **2b.** Ventral view of gamont.

**Figure 6.** 1–4. Ontogeny of *Planoglabratella opercularis* (d'Orbigny) both with and without peripheral spines. From Omaezaki Cape, Shizuoka Prefecture. Scale bar indicates 500  $\mu$ m. Dorsal (a) and ventral (b) views are shown for 1–4. **1a.** Agamont individuals without peripheral spines. **1b.** Agamont individuals without peripheral spines. **2a.** Gamont individuals without peripheral spines. **2b.** Gamont individuals without peripheral spines. **3a.** Agamont individuals with peripheral spines. **3b.** Agamont individuals with peripheral spines. **4a.** Gamont individuals with peripheral spines. **4b.** Gamont individuals with peripheral spines.



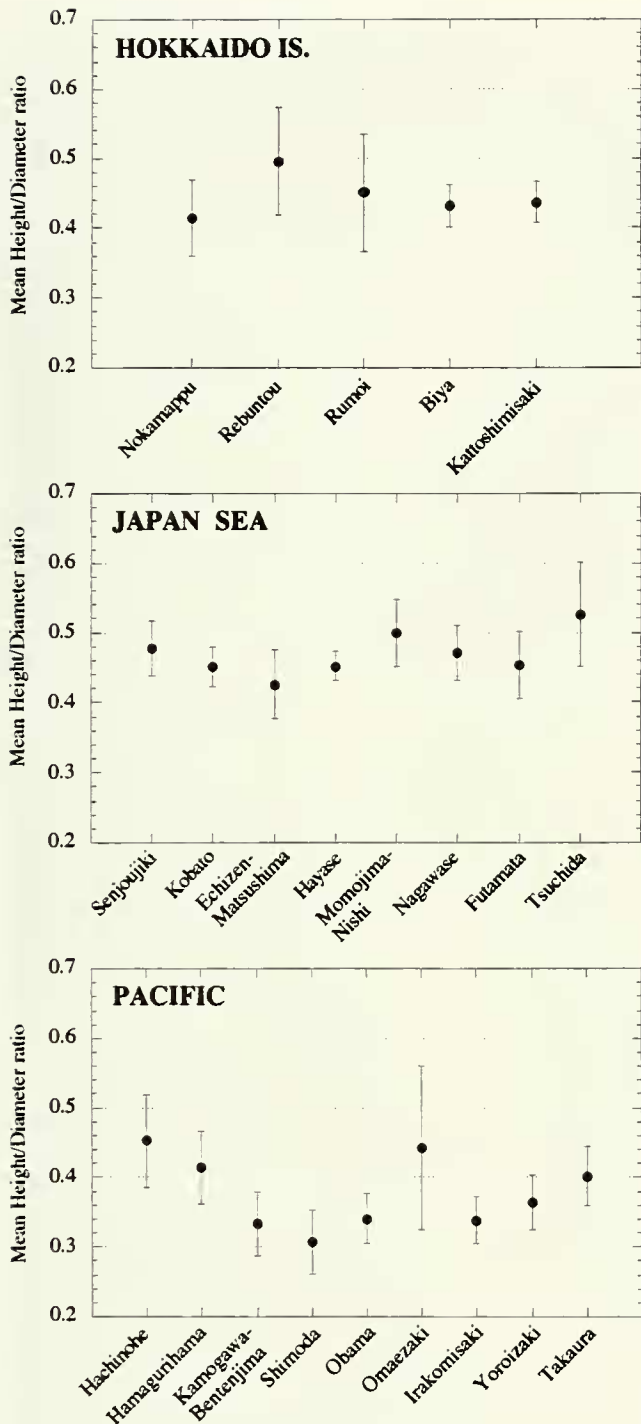


Figure 7. Geographic distributions of height/diameter ratio of *Planoglabratella opercularis* morphogroup around the Japanese Islands from various samples taken during different seasons. Black circles mask average height/diameter ratio at different localities. Bars straddling circles indicate the range of one standard deviation of data at each locality.

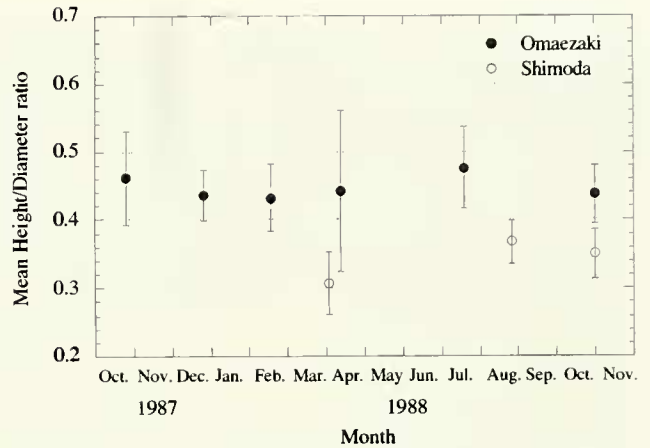


Figure 8. Seasonal differences of average height/diameter ratios of *Planoglabratella opercularis* both at Omaezaki Cape and Shimoda Bay, in Shizuoka Prefecture. Black circles show the data from Omaezaki Cape. Open circles show the data from Shimoda Bay. Bars indicate the range of one standard deviation of data at each locality.

*Glabratella* are mostly the same as those described by Le Calvez (1950) for *Discorbis mediterraneensis*.

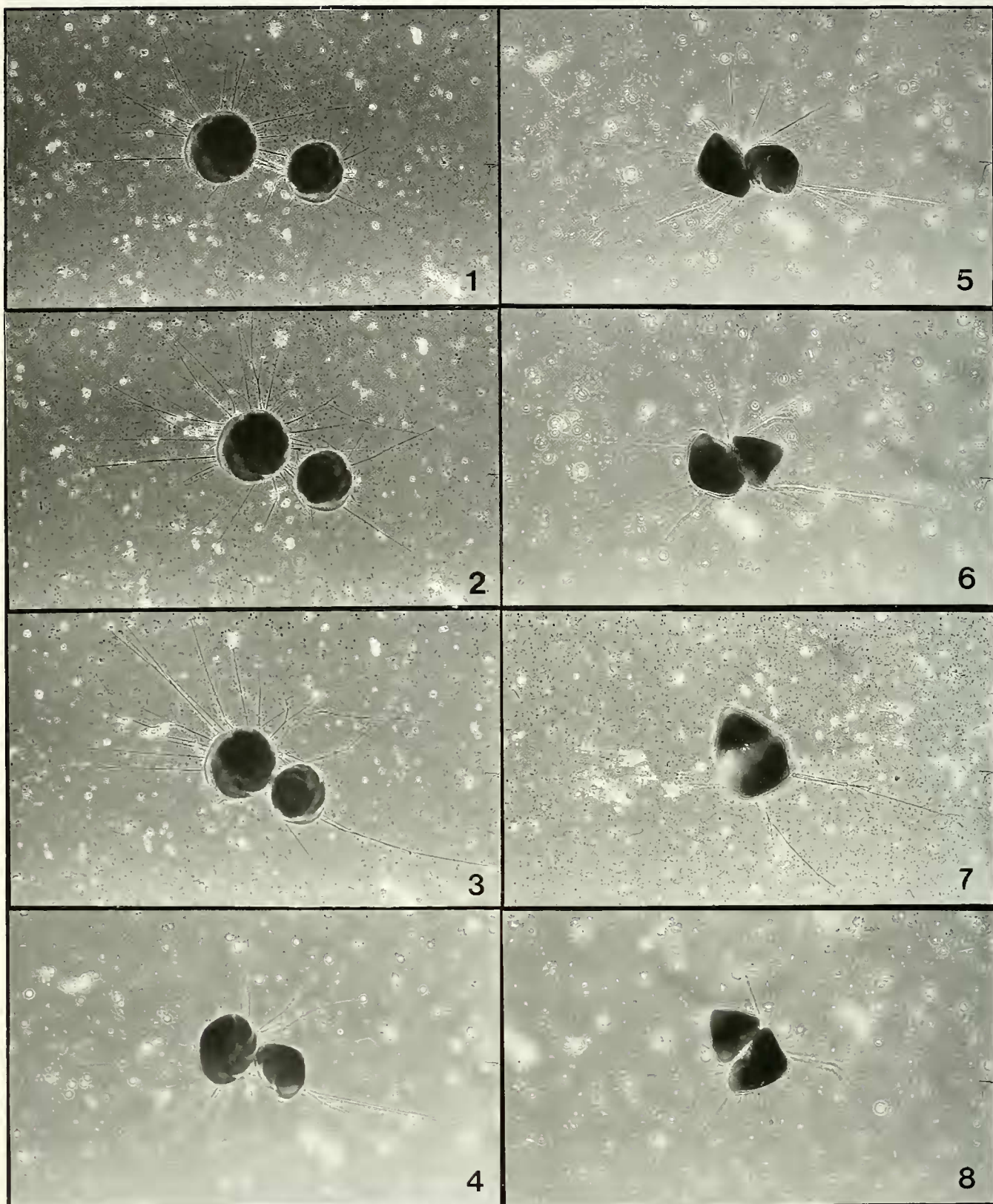
The results of the interbreeding experiments are summarized in Figure 10. Individuals that belonged to the same morphogroup mated, but those that belonged to separate morphogroups did not (Figure 10A). These results suggest that the species reclassified by morphology can probably be considered to be breeding populations.

However, there are individuals within the same population of a morphogroup that did not mate. Although they touched each other, they did not go further in forming a pair; instead, the rhizopods were disconnected and the individuals moved independently. The results indicate that some kinds of sexual differentiation may exist in *Glabratella*, as suggested by Le Calvez (1950), Grell (1957, 1958a, b, 1959), Weber (1965) and Berthold (1971) for several species that formed gamontogamous aggregates during fertilization.

Gamont individuals from the same parental agamont sometimes formed pairs; however, there was no exchange of gametes. This could mean that autogamy may not occur in *Glabratella*, even though autogamy has been found among species of the genus *Rotaliella* as described in Grell (1973).

Individuals from different morphogroups never reacted to each other, even if their rhizopodia were close enough to touch.

As described above, two morphological variations occur in *P. opercularis*, i. e., presence/absence of peripheral spines and height/diameter ratio. Both individuals with and without peripheral spines were able to form gamontogamous pairs and reproduced during culture experiments (Figure 10B). SEM photographs of a gamontogamous pair formed by a spinose and a nonspinose individual are shown in Figure 11. Both high and low trochospiral individuals also formed gamontogamous pairs (Figures 10B, 12.1, 12.2) and also re-





## A INTERSPECIFIC BREEDING EXPERIMENTS

	<i>P. nakamurai</i>	<i>P. opercularis</i>	<i>G. patelliformis</i>
<i>P. nakamurai</i>	7/18	0/48	0/22
<i>P. opercularis</i>		11/30	0/33
<i>G. patelliformis</i>			1/4

## B INTRASPECIFIC BREEDING EXPERIMENTS

### *Planoglabratella opercularis* (d'Orbigny)

	spinose	non-spinose	high H/D ratio	low H/D ratio
spinose	2/3	7/9	***	***
non-spinose		35/58	***	***
high H/D ratio			11/30	9/14
low H/D ratio				47/73

## C INTERPOPULATIONAL BREEDING EXPERIMENTS

### *Planoglabratella opercularis* (d'Orbigny)

	Echizen-Matsushima	Oshika Peninsula	Shimoda	Omaezaki
Echizen-Matsushima	1/3	***	***	0/3
Oshika Peninsula		2/6	***	0/6
Shimoda			47/73	10/61
Omaezaki				16/41

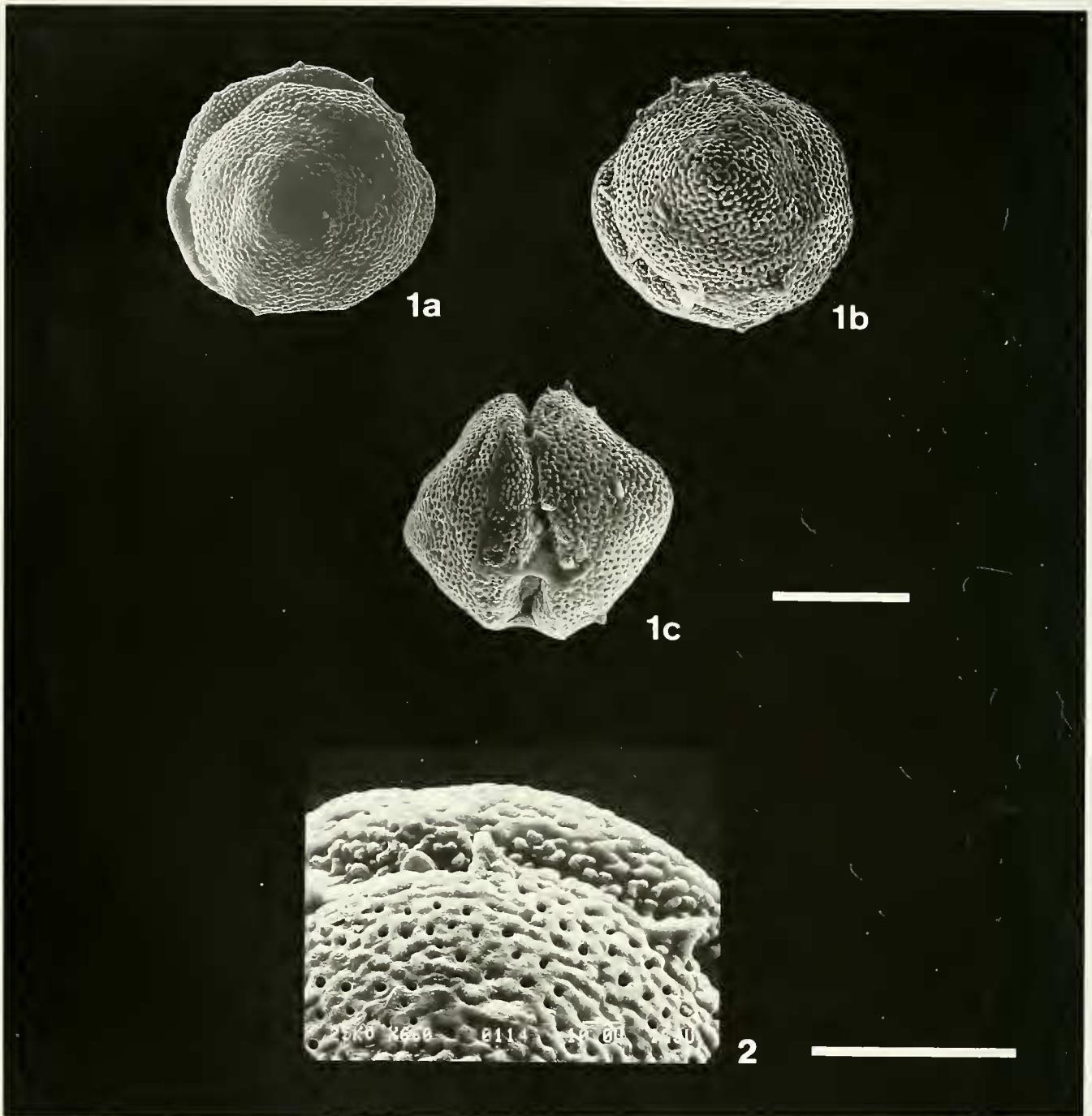
**Figure 10.** Results of interbreeding experiments with both inter- and intraspecific populations. Results of interpopulational breeding experiments are also shown. Numerals to the left of the slash show combinations that actually formed a gamontogamous pair. Numerals to the right of the slash indicate the number of experiments for each combination. \*\*\*: no experimental data. A. Interspecific breeding experiments, B. Intraspecific breeding experiments, C. Interpopulational breeding experiments.

produced (Figure 12.3, 12.4). These results clearly show that all variants belong to the same population and can interbreed. Both spines and H/D ratio were formerly used as key morphological characters for defining *Glabratella* species. We have not yet examined how these morphological characters appear in daughter or granddaughter cells.

Interbreeding experiments among *P. opercularis* populations from different localities indicate that geographically remote populations do not make gamontogamous pairs (Figures 10C, 13). Gamont specimens between Omaezaki

Cape and Shimoda Bay made gamontogamous pairs and reproduced. However, individuals between Omaezaki Cape and Oshika Peninsula, Miyagi Prefecture and between Omaezaki and Echizen-Matsushima Coast, Fukui Prefecture did not make gamontogamous pairs with each other, even though morphological characteristics of *P. opercularis* populations at the three localities are very similar. These interbreeding experiments of individuals of remotely separated populations show that the interbreeding abilities of populations are closely related to geographic distances between

**Figure 9.** Series of photographs showing the process of forming a gamontogamous pair of *Glabratella patelliformis* (Brady) on September 1, 1987. Photographed in 1. 1548 hours, 2. 1549 hours, 3. 1550 hours, 4. 1554 hours, 5. 1555 hours, 6. 1556 hours, 7. 1557 hours, 8. 1600 hours. Collected at Shimoda Bay, Shizuoka Prefecture.



**Figure 11.** Gamontogamous pair between individuals with peripheral spines and without spines of *Planoglabratella opercularis* (d'Orbigny). Scale bars for 1 a, b, c and for 2 indicate 100  $\mu\text{m}$  and 50  $\mu\text{m}$  respectively. 1a. Specimen without peripheral spines, 1b. Specimens with peripheral spines, 1c. Side view of gamontogamous pair. 2. Enlargement of peripheral spines.

**Figure 12.** Photographs showing the reproductive process of *Planoglabratella opercularis* (d'Orbigny) from a gamontogamous pair during culture experiments. 1. Gamontogamous pair between individual showing high height/diameter ratio of Omaezaki population and individual showing low height/diameter ratio of Shimoda population. Agamont juveniles are visible within one pair. Photographed at 2130 hours, November 4, 1988. 2. Side view of gamontogamous pair. Upper right individual shows higher height/diameter ratio than that of lower left individual. Photographed on November 4, 1988, 2140 hours. 3. Spreading of agamont offspring from the parental pair. Photographed on November 5, 1988. Juvenile agamonts have two chambers when they leave. 4. Juvenile agamont individuals with three chambers. Photographed on November 7, 1988.



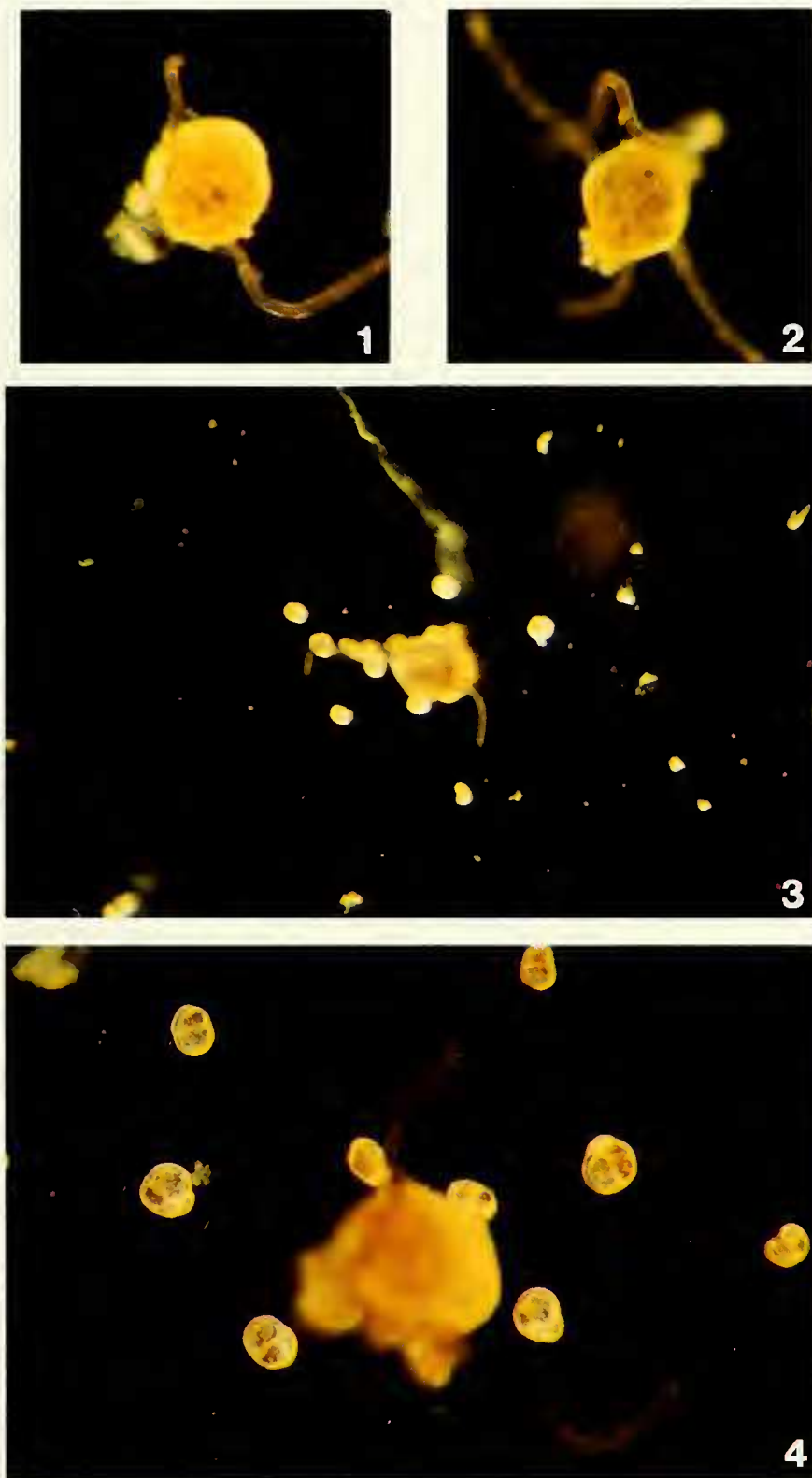
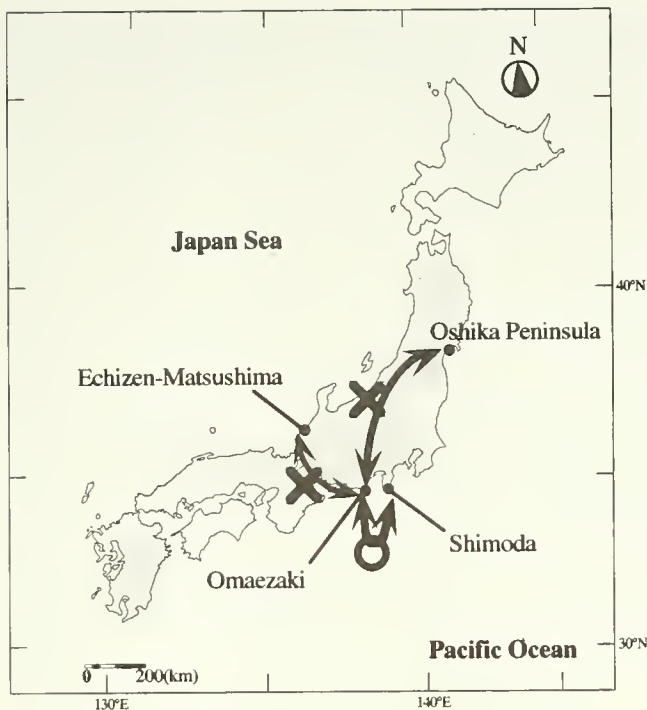


Figure 12.



**Figure 13.** Results of interbreeding experiments of individuals among geographically remote populations. Map shows localities from which individuals actually tried to interbreed. Circle and cross marks in the figure refer the populations that can and cannot interbreed, respectively. The results show that individuals from proximate localities can interbreed.

them. Individuals that succeeded in interbreeding belong to proximate populations. For instance, Omaezaki Cape is only 100 km from Shimoda Bay at the closest distance along the shoreline. In contrast, individuals from distant localities failed to interbreed. Oshika Peninsula is about 500 km from Omaezaki Cape. The Echizen-Matsushima Coast is more than 1000 km from Omaezaki Cape. Thus geographic distance is critical in determining interbreeding abilities among populations of a single morphospecies in *Glabratella*. This phenomenon suggests that populations of this glabratellan morphospecies have characteristics of ring species, with chains of local populations that can interbreed between neighboring populations.

### Summary

Four *Glabratella* morphospecies were reclassified into three morphogroups, according to stable morphological characters. There are several key morphological characters that are stable with ontogenetic stages, life cycle, and/or geographic distance. Certain morphological characters changed during ontogeny. Interbreeding experiments show that reclassified morphospecies can breed within one morphogroup. Several morphological characters are not stable during ontogeny. This shows that we cannot use every morphological feature to define *Glabratella* species.

Interbreeding experiments using individuals collected from geographically remote populations demonstrate that individuals of closely located populations can breed with each other, whereas individuals from distant populations cannot interbreed. These results suggest that glabratellan populations are chains of small, reproductively isolated populations.

Interbreeding experiments are a powerful tool to elucidate populational structure of morphologically defined species in foraminifera.

### Acknowledgments

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